Plant functional traits have globally consistent effects on competition

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Summary paragraph outline (234 / ideally of about 200 words, but certainly no more than 300 words)

Phenotypic traits and their associated trade-offs are thought to play an important role in community assembly and thus in maintaining species diversity. Although traits have been shown to have globally consistent effects on individual plant physiological function[1–3], it remains unclear whether these physiological effects scale-up to determine the outcomes of competitive interactions – a key driver of community assembly in terrestrial vegetation[4]. Here we use growth data from more than 3 million trees in more than 140000 plots across the world to show how three key functional traits – wood density, specific leaf area and maximum height – consistently influence competitive interactions. Both lower wood density and higher specific leaf area directly increased the maximum growth of a focal tree. At the same time, lower wood density reduced the ability of focal trees to tolerate competition, while higher specific leaf area reduced the competitive effect of that tree on its neighbours. Smaller than these effects, but still detectable for all three traits, was a limiting similarity effect, through which neighbouring plants suffered less from competition when they differed more strongly in their traits. By demonstrating at a global scale that traits generate trade-offs between performance with *vs.* without competition, we provide broad-scale support for the classic hypothesis that coexistence of plant species is enabled via differentiation in successional strategy[5]. In addition, our trait-based approach to modelling competition reveals generalisations across the forest ecosystems of the globe.

Main text (MAX 1500 words till the end of Main text = 1303)

Phenotypic traits are considered fundamental drivers of community assembly and thus species diversity. The effects of traits on individual plant physiology and function are increasingly understood, underpinned by well-known and globally consistent trade-offs[1–3]. For instance, traits such as wood density and specific leaf area capture trade-offs between the construction cost and longevity or strength of wood and leaf tissues[2,3]. In contrast, understanding of how trait-based trade-offs translate into competitive outcomes between species is still extremely limited, particularly for long-lived forest ecosystems. Competition is the key filter through which ecological and evolutionary success is determined[4]. The few studies[6–10] that have explored links between traits and competition have questioned the long-held idea that competition is stronger when two species have similar traits, instead proposing that particular trait values may confer competitive advantage[11]. This distinction is fundamental because if neighborhood competition is driven mainly by trait similarity, this will favour a wide spread of trait values at local scale, whereas if neighborhood interactions are mainly driven by the competitive advantage associated with particular trait values, those trait values should be strongly selected at the local scale, with coexistence operating at larger spatial or temporal scales[11,12]. However, thus far empirical investigations are limited to isolated and few locations, limiting our ability to establish generalisation about the mechanisms linking traits and competition in the main vegetation types of the world.

Here we quantify the links between traits and competition, measured as the influence of neighbours on growth of a focal tree. Our framework is novel in two important ways: (i) competition is analysed at an unprecedented scale covering all the major forest biomes on Earth (Fig. 1a) and (ii) the influence of traits on competition is partitioned among four fundamental mechanisms (Fig. 1b,c) as follows. A competitive advantage for some trait values compared to others can arise (1) through permitting faster maximum growth in absence of competition[13]; (2) through stronger competitive effect[14,15], competitor species possessing those traits reducing more strongly the growth of their neighbours; or (3) through better tolerance of competition (or competitive 'response' in Goldberg[14]), growth of species possessing those traits being less affected by competition from neighbours. Finally, (4) competition can promote trait diversification, if decreasing trait similarity between neighbouring trees weakens their competitive interactions (*i.e.* limiting similarity)[16]. Here we dissect how these four mechanisms are connected to three key traits that describe plant strategies worldwide[1–3]: wood density (an indicator of a trade-off between stem construction cost and strength), specific leaf area (SLA, an indicator of a trade-off between leaf construction cost and leaf longevity), and maximum height (an indicator of a trade-off between access to light and early reproduction). We analyze basal area growth (rate of increase in the area of the cross section of tree trunk at 1.3 m height) of more than 3 million trees in more than 140000 plots, representing more than 2500 species, covering all the major biomes of the earth (Fig. 1) with respect to species mean traits values extracted from the global TRY data base[17,18] and local data bases (see Methods). We analysed how maximum growth of each individual tree was reduced by the local abundance of competitors in its neighborhood[19] (measured as the sum of basal areas of competitors in m^2/ha), accounting for traits of both the focal tree and its competitors. This analysis allowed effect sizes to be estimated for each of the four pathways (Fig. 1c).

Across all biomes the strongest driver of individual growth was the local abundance of competitors, irrespective of their traits; positive parameters indicate that these neighbours had competitive rather than facilitative effect. Then parameters reported that some trait values led to a competitive advantage compared to others through different mechanism. Strongest were direct influences of traits on focal plant's maximum growth (*i.e.* in absence of competition, see Fig. 2 and Extended data Table 3), with the fastest growing species having low wood density and high SLA (Fig. 2). Then secondly, some trait values were associated with species having stronger competitive effect, or better tolerance of competition (Fig. 2). Taken together these two processes were in similar importance as the direct effects of traits on maximum growth (Extended data Table 3; Fig 2). Low SLA caused species to exert a strong competitive effect on their neighbors, whereas high wood density allowed species to be more tolerant of competition by neighbours. Finally, there was a small but consistent effect of trait similarity between focal and neighbour species, with greater similarity leading to stronger competitive suppression of growth (Fig. 2). This 'limiting similarity' effect has generally been hypothesized as the key mechanism by which traits affect competition, but has been rarely confirmed with field data[11]. Our analysis shows that at global scale this process is present but not dominant in magnitude. Analyses that allowed for different effects among biomes did not show strong evidence for any particular biome behaving consistently differently from the others (Fig. 2). Results varied most among biomes for SLA.

This may reflect fundamental differences between deciduous and evergreen plant lifeforms[20] (futher detail in Supplementary Discussion).

Importantly, our global study supports the hypothesis that trait values favouring high tolerance of competition or high competitive effect also render species slow growing in absence of competition across all forested biomes (Fig. 3). This trait-based trade-off is critical because it confirms the classical explanation for successional coexistence of species in forests in which fast-growing species dominate in open areas where competitors are absent, later being replaced by slow-growing species that dominate in closed vegetation where competitors are present[5]. Trade-offs were present for wood density and specific leaf area (Fig. 3). The directions of trait-effects underpinning them agreed well with existing literature (further detail in Supplementary Discussion). High wood density was associated with slow potential growth rate but high tolerance to competition (Fig. 3), in agreement with shade-tolerant species having high wood density[13]. High SLA was correlated with a fast maximum growth, as reported in previous studies of trees[13], but with a weakened competitive effect (Fig. 3), in agreement with the observation that the shorter leaf life span associated with high SLA results in low standing leaf area and low light interception[21]. Coordination between trait values conferring high competitive effect and trait values conferring high tolerance of competition has been generally expected[7,14]. However, we found little evidence for such coordination (see also references[22–24]). Only, wood density and specific leaf area had the same direction for their competitive effect and tolerance of competition parameters. However, confidence interval intercepting zero for one parameter for both traits (Fig. 2). Finally, the underlying mechanisms explaining for limiting similarity effect are unknown for these traits. This could include neighbouring species with similar traits supporting heavier loads of specialised pathogens[25], capturing light less efficiently because of less complementarity in architectural and temporal niche[26] or recycling litter less efficiently[27].

Analysing species interaction via interaction coefficients between pairs of species quickly become intractable in species rich communities, as the number of different interactions rises with the square of species number. Also this species-pair approach does not lead naturally to generalization across different vegetation types and different continents. The globally consistent links that we report here between traits and competition have considerable promise to overcome these problems, allowing us to predict complex species interactions governing forest communities at a global scale. A challenge for the future is to analyse survival and recruitment as well as growth on the basis of traits. This would span the whole life-cycle and build a more complete picture of the fitness consequences of different traits. These analysis of growth already demonstrate, that trait similarity is not the major determinant of local scale competition among plants (see also references[10–12]) and is thus not the central mechanisms explaining the coexistence of species with diverse traits. However at the regional scale, a mosaic of successional stages can favour different compromises along a trade-off axis between maximum growth and performance in conditions of high competition, supporting a diversity of traits in this way.

Supplementary Information is available in the online version of the paper.

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Author contributions GK and MW conceived the study and led a workshop to develop this analysis with the participation of DAC, DF, FH, RMK, DCL, LP, MV, GV, and JSW. GK wrote the manuscript with input from all authors. G.K. devised the main analytical approach, wrote the computer code and performed analyses. G.K. and F.H. processed the data. GK, DAC, DF, FH, RMK, DCL, MV, GV, JSW, MA, CB, JC, JHCC, SGF, MH, BH, JK, HK, YO, JP, HP, MU, SR, PRB, IFS, GS, NS, JT, BW, CW, MAZ, HZ, JZ, NEZ collected and processed the raw data.

Author information The authors declare no competing financial interests.

FIGURES & TABLES (legend total 489 /500 max words)

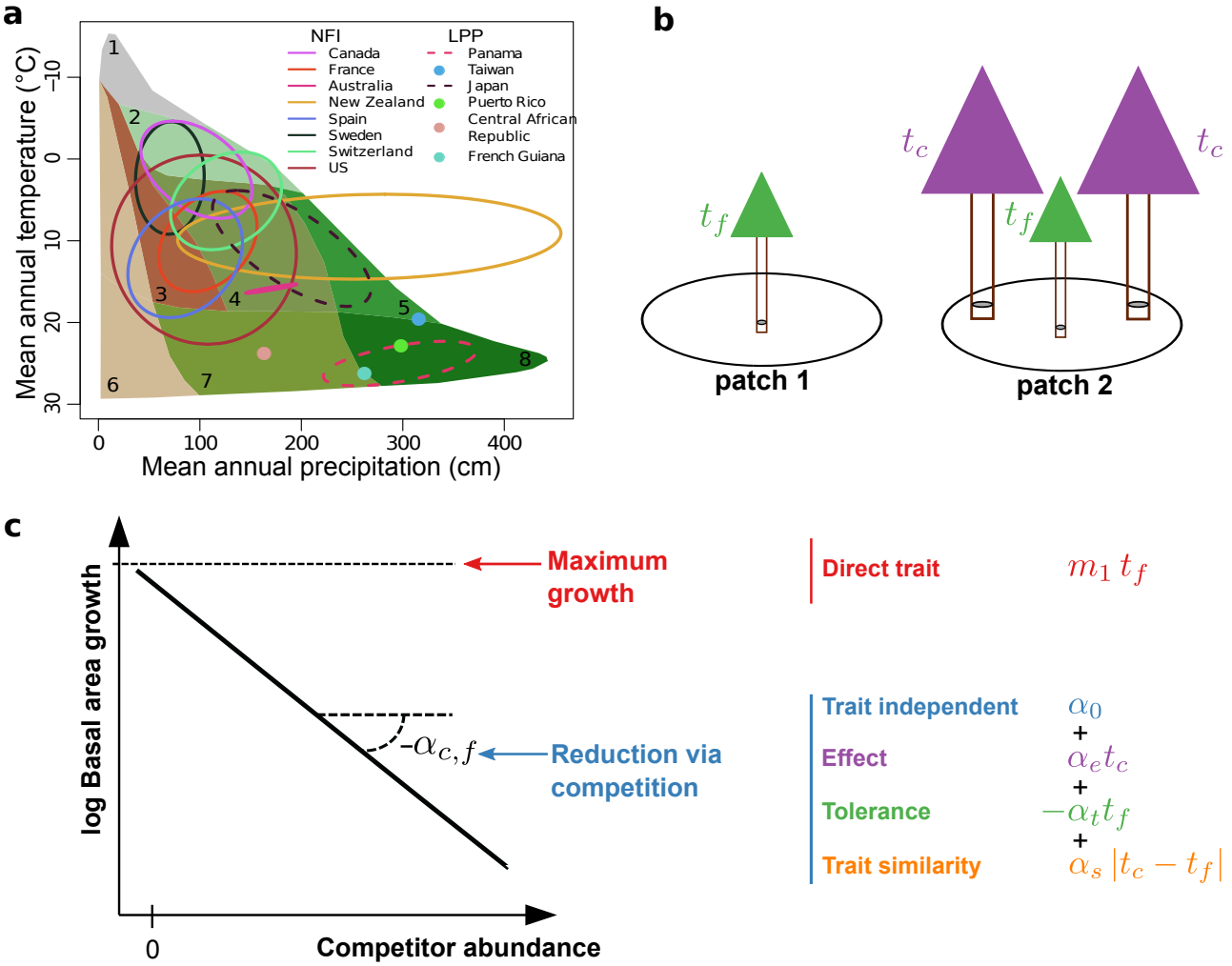

Figure 1: **Assessing competitive interactions at global scale.** **a,** Precipitation-temperature space occupied by each data set (NFI data : national forest inventories, LPP data : large permanent plots). For data with multiple plots, the range of climatic condition is represented by an ellipse covering 98% of the plots. Biomes are: 1, tundra; 2, taiga; 3, mediterranean; 4, temperate forest; 5, temperate rainforest; 6, desert; 7, tropical seasonal forest; 8, tropical rainforest (as defined by Ricklefs[28]). **b,** Sampled patches vary in the abundance of competitors from species c around individuals of focal species f. **c,** We modeled how trait values of the focal tree (t_f), and the abundance (measured as the sum of their basal areas) and traits values of competitors species (t_c) influence basal area growth of the focal tree. Maximum growth (red) is influenced by trait of the focal tree ($m_0 + m_1\, t_f$). Reduction in growth per unit basal area of competitor (blue, $-\alpha_{c,f}$) is modelled as the sum of growth reduction independent of trait (α_0), the effect of competitor traits (t_c) on their competitive effect (α_e), the effect of the focal tree's traits (t_f) on its tolerance of competition (α_t), and the effect of trait similarity between the focal tree and its competitors ($|t_c - t_f|$) on competition (α_s) ($\alpha_{c,f} = \alpha_0 + \alpha_e\, t_c - \alpha_t\, t_f + \alpha_s\, |t_c - t_f|$) . The parameters $m_0, m_1, \alpha_0, \alpha_e, \alpha_t$ and α_s are fitted from data using maximum likelihood method.

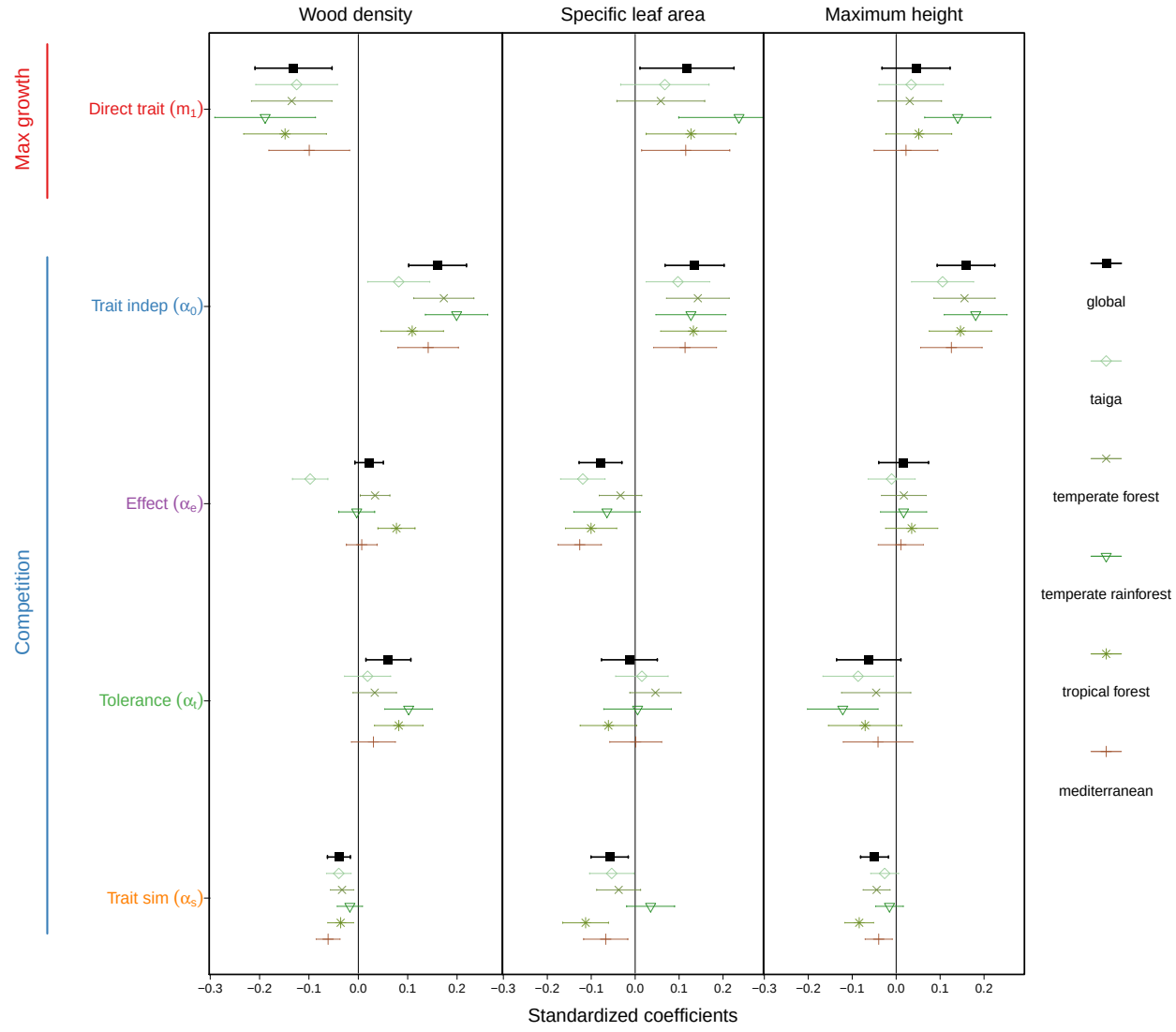

Figure 2: **Global trait effects and trait-independent effects on maximum growth and competition and their variation between biomes.** Standardized regression coefficients for growth models, fitted separately for each trait (points: mean estimates and lines: 95% confidence intervals). Black points and lines represent global estimates and coloured points and lines represents the biome level estimates. The parameter estimate represents: effect of focal-tree trait on maximum growth m_1, the competitive effect independent of traits α_0, the effect of competitor traits on their competitive effect α_e (positive value indicates that higher trait values lead to a stronger reduction in the growth of the focal tree), the effect of the focal tree's traits on its tolerance of competition α_t (positive value indicates that greater trait values result in greater tolerance of competition), and the effect on competition of trait similarity between the focal tree and its competitors α_s (negative value indicates that higher trait similarity leads to a stronger reduction of the growth of the focal tree). Tropical rainforest and tropical seasonal forest were merged together as tropical forest, tundra was merged with taiga, and desert was not included as too few data were available (see Fig 1a. for biomes definitions).

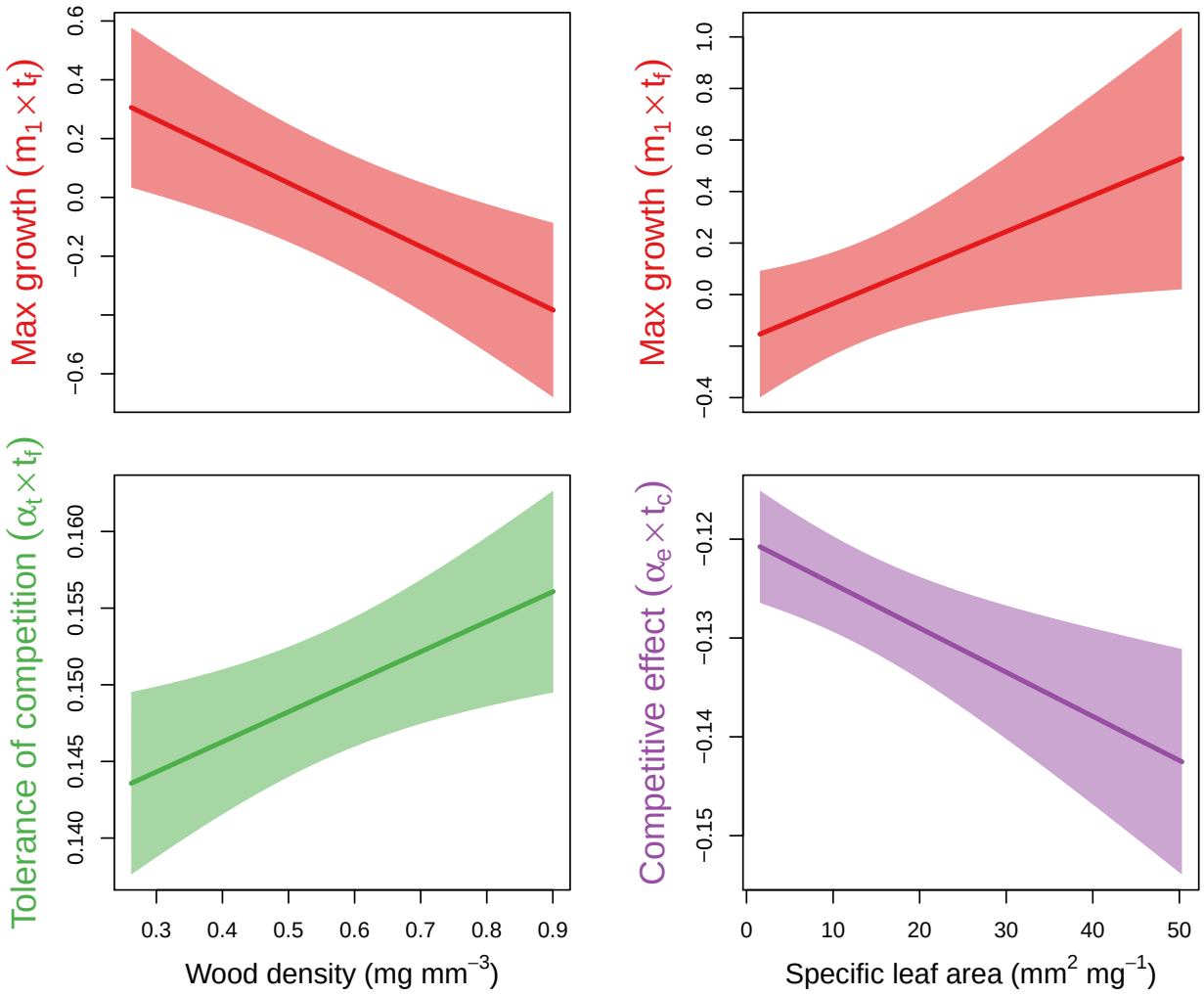

Figure 3: **Trade offs between maximum growth and competitive effect or competitive tolerance parameters for wood desnity and specific leaf area.** First column, variation of maximum growth rate ($m_1\, t_f$) and tolerance of competition ($\alpha_t\, t_f$) parameters with wood density. Second column, variation of the maximum growth rate ($m_1\, t_f$) and competitive tolerance ($\alpha_e\, t_c$) parameters with specific leaf area. The shaded area represents the 95% confidence interval of the prediction (including uncertainty associated with α_0 or m_0).

References (max 30)

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Methods (1497-without refs /max 3000 words)

Model and analysis

To examine the link between competition and traits we used a neighbourhood modelling framework[1–5] to model the growth of a focal tree of species f as a product of its maximum growth rate (determined by its traits and size) together with reductions due to competition from individuals growing in the local neighbourhood. Specifically, we assumed a relationship of the form

$$G_{i,f,p,s} = G_{\max f,p,s}\, D_i^{\gamma_f}\, \exp\left(\sum_{c=1}^{N_p} -\alpha_{c,f} B_{i,c,p,s}\right), \tag{1}$$

where:

- $G_{i,f,p,s}$ and $D_{i,f,p,s}$ are the the annual basal area growth and diameter at breast height of individual i from species f, plot p and data set s,
- $G_{\max f,p,s}$ is the potential growth rate in basal area growth for species f on plot p in data set s, i.e. in absence of competition,
- γ_f determines the rate at which growth changes with size for species f, modelled with a normally distributed random effect of species $\epsilon_{\gamma,f}$ [as $\gamma_f = \gamma_0 + \epsilon_{\gamma,f}$ where $\epsilon_{\gamma,f} \sim N(0, \sigma_\gamma)$]
- N_p is the number of competitor species on plot p ,
- $\alpha_{c,f}$ is the per unit basal area effect of individuals from species c on growth of an individual in species f, and
- $B_{i,c,p,s} = 0.25\,\pi \sum_{j \neq i} w_j\, D^2_{j,c,p,s}$ is the sum of basal area of all individuals trees j of the species c competiting with the tree i within the plot p and data set s, where w_j is a constant based on subplot size where tree j was measured. Note that $B_{i,c,p,s}$ include all trees in the plot excepted the tree i.

Values of $\alpha_{c,f} > 0$ indicate competition, whereas $\alpha_{c,f} < 0$ indicates facilitation.

Log-transformation of eq. 1 leads to a linearised model of the form

$$\log G_{i,f,p,s} = \log G_{\max f,p,s} + \gamma_f \log D_{i,f,p,s} + \sum_{c=1}^{N_p} -\alpha_{c,f} B_{i,c,p,s}. \tag{2}$$

To include the effect of a focal trees' traits, t_f, on its growth, we let:

$$\log G_{\max f,p,s} = m_0 + m_1\, t_f + \epsilon_{G_{\max},f} + \epsilon_{G_{\max},p} + \epsilon_{G_{\max},s}. \tag{3}$$

Here m_0 is the average maximum growth, m_1 gives the effect of the focal trees trait, and $\epsilon_{G_{\max},f}$, $\epsilon_{G_{\max},p}$, $\epsilon_{G_{\max},s}$ are normally distributed random effect for species f, plot or quadrat p (see below), and data set s [where $\epsilon_{G_{\max},f} \sim N(0, \sigma_{G_{\max},f})$; $\epsilon_{G_{\max},p} \sim N(0, \sigma_{G_{\max},p})$ and $\epsilon_{G_{\max},s} \sim N(0, \sigma_{G_{\max},s})$].

To include trait effects on competition presented in Fig. 1, competitive interactions were modelled using an equation of the form[1]:

$$\alpha_{c,f} = \alpha_{0,f} - \alpha_t\, t_f + \alpha_e\, t_c + \alpha_s\, |t_c - t_f| \tag{4}$$

where:

- $\alpha_{0,f}$ is the trait independent competition for the focal species f, modelled with a normally distributed random effect of species f and a normally distributed random effect of data set s [as $\alpha_{0,f} = \alpha_0 + \epsilon_{\alpha_0,f} + \epsilon_{\alpha_0,s}$, where $\epsilon_{\alpha_0,f} \sim N(0, \sigma_{\alpha_0,f})$ and $\epsilon_{\alpha_0,s} \sim N(0, \sigma_{\alpha_0,s})$],
- α_t is the **tolerance of competition** of the focal species, i.e. change in competition tolerance due to traits t_f of the focal tree with a normally distributed random effect of data set s included [$\epsilon_{\alpha_t,s} \sim N(0, \sigma_{\alpha_t})$],
- α_e is the **competitive effect**, i.e. change in competition effect due to traits t_c of the competitor tree with a normally distributed random effect of data set s included [$\epsilon_{\alpha_i,s} \sim N(0, \sigma_{\alpha_i})$], and
- α_s is the effect of **trait similarity**, i.e. change in competition due to absolute distance between traits $|t_c - t_f|$ with a normally distributed random effect of data set s included [$\epsilon_{\alpha_s,s} \sim N(0, \sigma_{\alpha_s})$].

Eqs. 2-4 were then fitted to empirical estimates of growth, given by

$$G_{i,f,p,s} = 0.25\pi \left(D^2_{i,f,p,s,t+1} - D^2_{i,f,p,s,t} \right). \tag{5}$$

To estimate standardised coefficients (one type of standardised effect size)[6], response and explanatory variables were standardized (divided by their standard deviations) prior to analysis. Trait and diameter were also centred to facilitate convergence. The models were fitted using *lmer* in lme4[7] with R[8]. We fitted two versions of this model. In the first version parameters $m_0, m_1, \alpha_0, \alpha_t, \alpha_i, \alpha_s$ were estimated as constant across all biomes. In the second version, we repeated the same analysis as the first version but provided for different fixed estimates of these parameters for each biome. This enabled us to explore variation between biomes. Because some biomes had few observations, we merged some biomes with

[1]For fitting the model the equation of $\alpha_{c,f}$ was developped with species basal area in term of community weighted mean of the trait, see Supplementary methods for more details.

similar climate. Tundra was merged with taiga, tropical rainforest and tropical seasonal forest were merged into tropical forest, and deserts were not included in this final analysis as too few data were available.

Data

Growth data

Our main objective was to collate data sets spanning the dominant forest biomes of the world. Data sets were included if they (i) allowed both growth rate of individual trees and the local abundance of competitors to be estimated, and (ii) had good (>40%) coverage for at least one of the traits of interest (SLA, wood density, and maximum height).

The data sets collated fell into two broad categories: (1) national forest inventories (NFI), in which trees above a given diameter were sampled in a network of small plots (often on a regular grid) covering the country (references of NFI data used[9–18]); (2) large permanent plots (LPP) ranging in size from 0.5-50ha, in which the x-y coordinates of all trees above a given diameter were recorded (references of LPP data used[19–26]). These LPP were mostly located in tropical regions. The minimum diameter of recorded trees varied among sites from 1-12cm. To allow comparison between data sets, we restricted our analysis to trees greater than 10cm. Moreover, we excluded from the analysis any plots with harvesting during the growth measurement period, that were identified as a plantations, or overlapping a forest edge. Finally, we selected only two consecutive census dates for each tree to avoid having to account for repeated measurements, as less than a third of the data had repeated measurements. See the Supplementary Methods and Extended Data Table 1 for more details on the individual data sets.

Basal area growth was estimated from diameter measurements recorded across successive time points. For the French NFI, these data were obtained from short tree cores. For all other data sets, diameter at breast height (D) of each individual was recorded at multiple census dates. We excluded trees (i) with extreme positive or negative diameter growth rates, following criteria developed at the BCI site[20] (see the R package CTFS R), (ii) that were a palm or a tree fern species, or (iii) that were measured at different height in two consecutive censuses.

For each individual tree, we estimated the local abundance of competitor species as the sum of basal area for all individuals > 10cm diameter within a specified neighbourhood. For LPPs, we defined the neighbourhood as being a circle with 15m radius. This value was selected based on previous studies showing the maximum radius of interaction to lie in the range 10-20m[2,27]. To avoid edge effects, we also excluded trees less than 15m from the edge of a plot. To account for variation of abiotic conditions within the LPPs, we divided plots into regularly spaced 20x20m quadrats.

For NFI data coordinates of individual trees within plots were generally not available, thus neighbour-

hoods were defined based on plot size. In the NFI from the United States, four sub-plots of 7.35m located within 20m of one another were measured. We grouped these sub-plots to give a single estimate of the local competitor abundance. Thus, the neighbourhoods used in the competition analysis ranged in size from 10-25 m radius, with most plots 10-15 m radius.

We extracted mean annual temperature (MAT) and mean annual sum of precipitation (MAP) from the worldclim data base[28], using the plot latitude and longitude. MAT and MAP data were then used to classify plots into biomes, using the diagram provided by Ricklefs[29] (after Whittaker).

Traits

Data on species functional traits were extracted from existing sources. We focused on wood density, species specific leaf area (SLA) and maximum height, because these traits have previously been related to competitive interactions and are available for large numbers of species[2–5,30] (see Extended data Table 2 for traits coverage). Where available we used data collected locally (References for the local traits data used in this analysis[21,30–33]); otherwise we sourced data from the TRY trait data base[34] (References for the data extracted from the TRY database used in this analysis[30,35–104]). Local data were available for most tropical sites and species (see Supplementary methods). Several of the NFI data sets also provided tree height measurements, from which we computed a species' maximum height as the 99% quantile of observed values (for France, US, Spain, Switzerland). For Sweden we used the estimate from the French data set and for Canada we used the estimate from the US data set. Otherwise, we extracted measurement from the TRY database. We were not able to account for trait variability within species between sites.

For each focal tree, our approach required us to also account for the traits of all competitors present in the neighbourhood. Most of our plots had good coverage of competitors, but inevitably there were some trees where trait data were lacking. In these cases we estimated trait data as follows. If possible, we used the genus mean, and if no genus data was available, we used the mean of the species present in the country. However, we restricted our analysis to plots where (i) the percentage of basal area of trees with no species level trait data was less than 10%, and (ii) no genus level data was less than 5%.

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